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THE EFFECT OF SIMULATED ACIDIC RAIN ON FIRST-SEASON SEEDLINGS OF PINUS CONTORTA SSP. LATIFOLIA

by
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The Effect of Simulated Acidic Rain on First-season Seedlings of *Pinus contorta* ssp. *latifolia*

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Abstract

To assess the effect of acidic precipitation on seedlings growing in native soils, simulated acidic rain was applied to seeds of lodgepole pine in a greenhouse environment. Rain treatments were formulated by adding HNO_3 or HCl to simulated ambient rainfall from Rocky Mountain National Park. Seedlings treated with high levels of HNO_3 showed significant increases in height, number of lateral buds, shoot biomass and root area and biomass when compared to controls, indicating a fertilization effect from the NO_3^- component. However, seedlings which showed enhanced growth also exhibited lower root to shoot ratios than controls, and had lower water potentials than controls following an eight-day drought. Hence, seedlings exposed to high levels of HNO_3, though larger, were more susceptible to drought.

Introduction

Lodgepole pine (*Pinus contorta* ssp. *latifolia*) typically grows on relatively dry and infertile sites (Alexander 1974). During the critical stages of germination and establishment, lodgepole seedlings may be subjected to drought or nutrient stress. Acidic rain may be an additional stress at this time (Macdonald et. al. 1986). The Rocky Mountain region may experience increased nitric acid deposition due to continued urbanization and associated increases in hydrocarbons and oxides

of nitrogen from auto emissions.

Effects of acidic rain on plants have been widely investigated, with much of the research focused on effects on growth and morphology of conifer seedlings (Wood and Bormann 1977; Lee and Weber 1979; McColl and Johnson 1983; MacDonald et al 1986; Percy 1986; Abouguendia and Bascak 1987). All of these studies used HNO_3 and H_2SO_4 as the primary "pollutants" in the acid rain chemistry. Results of these studies have generally shown no significant growth effects except at very low pH values. Effects have included increased root and shoot biomass (Wood and Bormann 1977), foliar damage (McColl and Johnson 1983), increased above-ground and reduced below-ground biomass (MacDonald et al. 1986), reduced height growth (Percy 1986) and reduction of foliar chlorophyll b (Abouguendia and Bascak 1987). In most cases, enhanced growth effects have been attributed to nitrogen fertilization via HNO_3, while growth reductions or foliar damage have been linked to increased H+ concentration.

The objective of this study was to determine the effect of simulated nitric acid rain on first-season lodgepole pine seedlings growing in native soils. Specifically, we investigated how increased nitric acidic rain might affect growth and drought tolerance. Effects on growth are particularly important because first-year conifer seedlings can rapidly deplete seed reserves and become dependent on first-year foliage for photosynthate (Kramer and Kozlowski, 1979). The effects of acidic rain on drought tolerance may be important because high mortality of

first-year lodgepole pine seedlings in natural habitats has been attributed to drought (Nobel, 1979). In addition, we utilized rain treatments that enabled us to delineate between NO_3^- mediated effects and effects due to increased H^+ concentration.

Methods and Materials

Experiments were conducted in the Colorado State University greenhouses. Six simulated rain treatments and two soil treatments were utilized in this study for a total of twelve rain/soil treatment combinations. Seedlings were grown in individual pots (5.5 x 5.5 x 9 cm). Each treatment combination consisted of 168 seedlings divided among 8 flats for a total of 2,016 seedlings. Flats were distributed on one bench in the greenhouse and rotated once a week.

The six simulated acidic rain (SAR) treatments consisted of one ambient (control), three HNO_3 and two HCl treatments. The ambient rain chemistry simulated rainwater in Rocky Mountain National Park during the summer of 1984 and 1985 (Schoettle and Hubbard, in review). The three HNO_3 treatments increased ambient NO_3^- 10, 30, and 50 times (10x NO_3^-, 30x NO_3^-, 50x NO_3^-) via the addition of HNO_3, with a concomitant decline in pH. The pH levels for the ambient, 10x, 30x, and 50x NO_3^- treatments were 4.6, 3.6, 3.1, and 2.9, respectively. The two HCl treatments were utilized to mimic the H^+ concentration in the 30x and 50x NO_3^- treatments so that a distinction could be made between seedling response to

acidity or NO_3^-. Rain treatments were applied twice a week via a rain simulator (Schoettle and Hubbard, in review). The rain simulator consisted of four treatment stalls with droplet size, intensity, and delivery rate being comparable between stalls. Droplet size is also comparable to that of ambient rainfall. Each stall was equipped with a turntable to ensure even distribution of simulated rain among seedlings. Treatments were rotated through the stalls for each rain event. Rain events delivered .8 cm of simulated rainfall for a total of 1.68 cm of rain applied weekly. The total amount of NO_3^- applied for the entire growth period in the ambient treatment was 1.22 mg.

Soil treatments consisted of two different soils from lodgepole pine forests in southern Wyoming (Albany and Fox Park). The top 26 cm of mineral soil was collected and sieved through .64 cm hardware cloth to remove large rocks and roots.

Seeds for the study were obtained from the US Forest Service's Albuquerque seed storage bank. The seeds were collected from the White River National Forest in 1980 at an elevation of 2,740 m. The seeds were stored at 4°C until planting.

Seeds were planted and grown with SAR treatments for 15 weeks. Weekly measurements were made of height and bud number on forty seedlings per treatment. At the end of the growth period, the 40 seedlings per treatment were harvested and a number of measurements were made. These included final height, total number of lateral buds, and total, above-, and below-ground biomass.

Root to shoot ratios were calculated, and relative root area was obtained using an area meter with methods described by Rietveld (1989).

To assess the effect of SAR on drought tolerance, representative seedlings were chosen after 13 weeks of growth and subjected to an eight day drought. At the end of the drought period, seedlings were clipped at ground level and pre-dawn water potentials were taken using a pressure bomb. Water potentials were measured on 5 seedlings per treatment.

Statistical analyses were conducted using SPSS (SPSS Inc.) statistical software. All data were evaluated for normality and homogeneity of variance. Data that did not vary homogeneously were log-transformed. Log-transformed data that did not vary homogeneously was evaluated using a procedure which does not rely on homogeneous variance (see below).

Two factor analysis of variance was used to determine if there was a significant soil by treatment interaction. One factor analysis of variance was used to determine significant treatment effects within each soil type. Tukey's HSD test was used to evaluate significant differences between treatments with homogeneous data. Dunnett's multiple comparison procedure was used to determine significant differences between non-homogeneous data. Orthogonal polynomials were fitted to data from seedlings exposed to the ambient and increased NO_3^- treatments to determine if seedling responses to these treatments were linear or quadratic. A separate regression equation including the linear

and quadratic (if significant) terms was fitted to the data to allow extrapolation to other treatment levels.

Results

There was a significant soil by treatment interaction ($p < 0.001$). In general, the seedlings grown in soil from Fox Park grew much better than those in soil from Albany. Because of this significant interaction, all subsequent analyses of growth and drought tolerance are within each soil type only.

Both Albany and Fox Park seedlings showed significant differences in their height growth when exposed to different SAR treatments (Figure 1). Albany seedlings exposed to 10x, 30x, and 50x NO_3^- treatments showed significant increases in their height growth when compared to ambient controls ($p < 0.05$), whereas HCl-treated seedlings were not significantly different from ambient controls. Fox Park seedlings exhibited a slightly different response. Seedlings exposed to 30x and 50x NO_3^- treatments were significantly different from ambient controls, but 10x NO_3^--treated seedlings were not ($p < 0.05$). Fox Park seedlings exposed to 50x HCl treatments were significantly different from ambient-treated seedlings ($p < 0.05$), while 30x HCl treatments were not.

Total numbers of lateral buds at the end of the growth period were significantly different among treatments for both Fox Park and Albany seedlings (Figure 2). Albany seedlings that were

exposed to 10x, 30x, and 50x NO_3^- treatments had significantly greater numbers of lateral buds than seedlings treated with ambient rain chemistry ($p < 0.05$). Albany seedlings treated with 30x HCl did not differ significantly from ambient controls, whereas there were significantly more lateral buds on seedlings exposed to 50x HCl treatments. In Fox Park soil, seedlings treated with 10x, 30x, and 50x NO_3^- had significantly more lateral buds than did ambient controls ($p< 0.05$). Seedlings exposed to the 30x HCl treatments did not show an increase in lateral bud number over ambient controls, but those treated with 50x HCl did ($p< 0.05$).

Total, above-, and below-ground biomass values for Albany and Fox Park seedlings are shown in Figures 3-5, respectively. Albany seedlings exhibited significant differences in their total biomass at all treatment levels when compared to ambient controls. With the exception of the 10x NO_3^- treatment, Fox Park seedlings also exhibited significantly greater total biomass at all treatment levels when compared to the ambient-treated seedlings ($p< 0.05$).

Not surprisingly, above- and below-ground biomass data show similar results. For Albany seedlings, all treatment levels were significantly different from ambient with respect to above- and below-ground biomass. In Fox Park seedlings above-ground biomass was also significantly greater at all treatment levels. For below-ground biomass, those seedlings exposed to 30x and 50x NO_3^- and 30x HCl treatments showed significant increases relative

to controls ($p < 0.05$).

Relative root area data for Albany and Fox Park seedlings are shown in Figure 6. For the Albany seedlings, all of the increased NO_3^- treatments showed significant increases ($p < 0.05$) in relative root area over ambient controls. The HCl-treated seedlings showed no significant differences. Fox Park seedlings showed significantly increased relative root area when treated with 30x NO_3^-, 50x NO_3^-, and 30x HCl. Seedlings treated with 10x NO_3^- and 50x HCl showed no significant differences in root area when compared to ambient controls.

Mean root to shoot ratios are shown in Figure 7. Albany seedlings treated with 30x and 50x NO_3^- exhibited a significant reduction in their root to shoot ratio when compared to ambient controls. The root to shoot ratios of seedlings exposed to HCl rain treatments were not significantly different from control seedlings. Fox Park seedlings exposed to 30x and 50x NO_3^- treatments also had significantly lower root to shoot ratios ($p < 0.05$). Seedlings exposed to 50x HCl treatments had significantly lower root to shoot ratios ($p < 0.05$) than controls, while seedlings treated with 10x NO_3^- and 30x HCl rain did not.

Mean pre-dawn water potentials taken at the end of an eight-day drought are shown in Figure 8. Albany seedlings that were exposed to 30x NO_3^-, 50x NO_3^-, and 50x HCl treatments had significantly lower (more negative) water potentials than ambient controls. All other treatment levels showed no significant differences in their water potentials when compared to ambient

controls. There were no significant differences in pre-dawn water potentials among treatments for Fox Park seedlings.

Response of Albany seedlings to increased NO_3^- was quadratic for all parameters measured, including water potential. The residuals for the quadratic model were only significant for root to shoot ratio data ($p< 0.001$).

Fox Park seedling response to increased NO_3^- treatments was slightly different. Response was quadratic for all parameters with the exception of lateral bud number and shoot biomass, which showed linear increases. Residuals were significant for total biomass ($p< 0.003$), shoot biomass ($p< 0.01$), root biomass ($p< 0.01$) and relative root area ($p< 0.01$). Equations for the quadratic and linear models for Albany and Fox Park seedlings are shown in the captions of Figures 1-8.

Discussion

Increases in growth of lodgepole pine seedlings exposed to simulated acidic rain appear to be in response to the NO_3^- component of our acid rain treatments. Although there is some increase in growth of seedlings exposed to increased H^+ concentrations (Fig. 1-4), the overall trend indicates that the NO_3^- is primarily responsible for increased growth. The reason for the acidity response is not known. However, enhanced microbial activity or increased availability of some limiting nutrient due to increased soil acidity are possible explanations.

Increased growth of first-year seedlings of lodgepole pine is one effect of simulated nitric acid rain. Lodgepole pine seedlings seem to be able to make use of the added NO_3^- to increase in height, biomass and the number of lateral buds. Increases in these parameters alone may enhance a seedling's ability to become established in the natural environment. Because of the relatively slow rate of root growth in lodgepole pine seedlings, survival may depend on the ability of seedlings to establish an adequate root system in the first-year (Alexander 1974). Nobel (1979) found that shallow rooting depth of first-year lodgepole pine seedlings was a major factor contributing to mortality. Larger root biomass and area from increased deposition of NO_3^- could enhance first-year seedling establishment. Similarly, because seedlings can rapidly exhaust seed reserves and become dependent on photosynthate from first-year foliage (Kramer and Kozlowski (1979), an increase in ability to produce more above-ground biomass may be beneficial.

Although root biomass, shoot biomass and relative root area all increased with increased NO_3^- concentration, the relative balance between shoot growth and root growth was altered significantly in seedlings from both Albany and Fox Park subjected to 30x NO_3^- and 50x NO_3^- treatments (Figure 7). Lower root to shoot ratios have been shown to be a common response to fertilization (Jones 1968, Zimmerman and Brown 1971, van den Driessche 1980). It appears that the lowered root/shoot ratios in this study are a result of the NO_3^- component of our simulated

acid rain chemistry. Ekwebelam and Reid (1984) similarly found that lodgepole pine seedlings had lower root/shoot ratios when subjected to high levels of ammonium-nitrate fertilizer. Etter (1969) also found lowered root/shoot ratios in lodgepole pine in response to nitrogen fertilization.

Such an imbalance between root growth and shoot growth may increase the susceptibility of seedlings to drought, since a larger transpirational surface is coupled with a relatively smaller absorptive root system. Data from the eight-day drought indicate that seedlings in which the root/shoot imbalance was most pronounced (30x NO_3^- and 50x NO_3^- Albany seedlings) had significantly lower pre-dawn water potentials than controls. Although the pre-dawn water potentials of Fox Park seedlings treated with 30x and 50x nitric acid rain appear to be lower than controls, the differences were not significant ($p= 0.06$). At the end of the drought period, Fox Park seedlings were not as drought stressed as Albany seedlings, i.e., they had less negative pre-dawn water potentials. Had the drought period been extended, significant differences similar to those found for Albany may have occurred in Fox Park seedlings. These results indicate that high concentrations of HNO_3, while increasing biomass production, reduce the drought tolerance of lodgepole pine seedlings growing in native soils. Although increases in HNO_3 deposition to levels 30x and 50x ambient may be unrealistic, increases in the range of 10x ambient levels may occur more readily.

Increased HNO_3 deposition in the 10x ambient range may affect the growth and drought tolerance of lodgepole pine seedlings. All Albany seedlings exhibited significantly increased growth when exposed to 10x ambient NO_3^- SAR. Root to shoot ratios and water potentials of 10x NO_3^- treated seedlings were lower than ambient controls but not significantly so. Our data suggest the possibility that unbalanced production of above- and below-ground biomass may lead to decreased drought tolerance in young lodgepole pine seedlings if deposition of NO_3^- increases significantly in the Rocky Mountain Region.

Conclusions

1. First-year seedlings of lodgepole pine grown in native soils exhibited dramatic increases in above- and below-ground growth when subjected to high levels of HNO_3. Comparisons with seedlings subjected to HCl treatments suggest that the enhancement of growth was due to a fertilization effect from the NO_3^- component of our acidic rain chemistry.

2. The enhancement of seedling growth at high levels of HNO_3 was accompanied by a decrease in root to shoot ratio, indicating a relative imbalance between root and shoot growth.

3. Lowered root to shoot ratios in seedlings subjected to high levels of HNO_3 resulted in reduced drought tolerance.

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Figure Captions

1. Mean total height for seedlings grown in soils from Albany or Fox Park, Wyoming. Treatments which do not share a common letter are significantly different ($p < 0.05$). A significant quadratic increase in height ($p < 0.05$) occurred in Albany seedlings exposed to simulated nitric acid rain. Fox Park seedlings also exhibited a significant quadratic increase in height ($p < 0.05$).

2. Mean total lateral bud number for seedlings grown in soils from Albany or Fox Park, Wyoming. Treatments which do not share a common letter are significantly different ($p < 0.05$). A significant quadratic increase in total bud number ($p < 0.05$) occurred in Albany seedlings exposed to simulated nitric acid rain. Fox Park exhibited a significant linear increase in total bud number ($p < 0.05$).

3. Mean total biomass for seedlings grown in soils from Albany or Fox Park, Wyoming. Treatments which do not share a common letter are significantly different ($p < 0.05$). A significant quadratic increase in total biomass ($p < 0.05$) occurred in Albany seedlings exposed to simulated nitric acid rain. Fox Park seedlings also exhibited a significant quadratic increase in total biomass ($p < 0.05$).

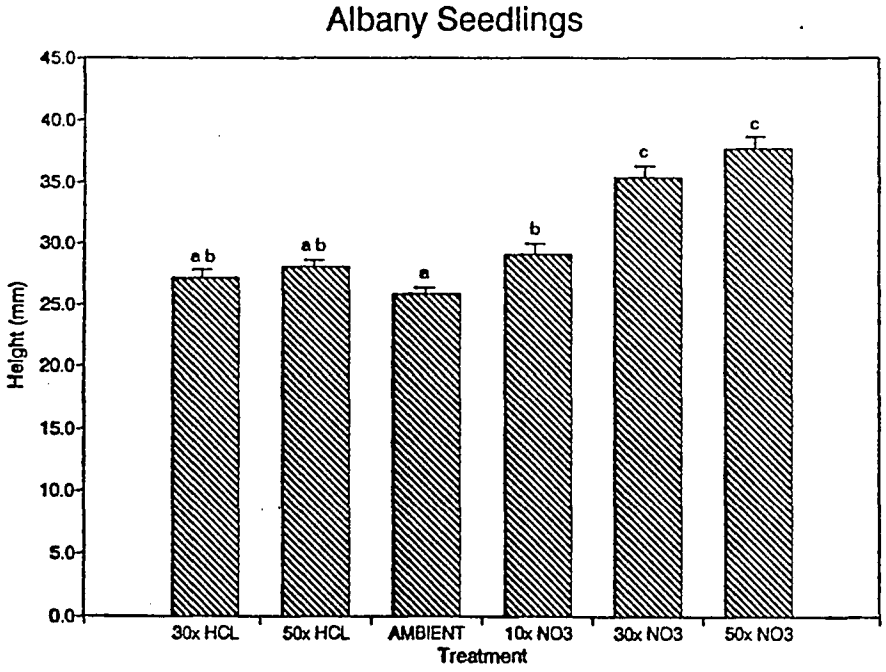
4. Mean shoot biomass for seedlings grown in soils from Albany or Fox Park, Wyoming. Treatments which do not share a common letter are significantly different ($p < 0.05$). A significant quadratic increase in shoot biomass ($p < 0.05$) occurred in Albany seedlings exposed to simulated nitric acid rain. Fox Park seedlings exhibited a significant linear increase in shoot biomass ($p < 0.05$).

5. Mean root biomass for seedlings grown in soils from Albany or Fox Park, Wyoming. Treatments which do not share a common letter are significantly different ($p < 0.05$). A significant quadratic increase in root biomass ($p < 0.05$) occurred in Albany seedlings exposed to simulated nitric acid rain. Fox Park seedlings also exhibited a significant quadratic increase in root biomass ($p < 0.05$).

6. Mean relative root area for seedlings grown in soils from Albany or Fox Park, Wyoming. Treatments which do not share a common letter are significantly different ($p < 0.05$). A significant quadratic increase in relative root area ($p < 0.05$) occurred in Albany seedlings exposed to simulated nitric acid rain. Fox Park seedlings also exhibited a significant quadratic increase in relative root area ($p < 0.05$).

7. Mean root to shoot ratios for seedlings grown in soils from Albany or Fox Park, Wyoming. Treatments which do not share a common letter are significantly different ($p < 0.05$). A significant quadratic decrease in root to shoot ratio ($p < 0.05$) occurred in Albany seedlings exposed to simulated nitric acid rain. Fox Park seedlings exhibited a significant linear decrease in root to shoot ratio ($p < 0.05$).

8. Mean pre-dawn water potentials for seedlings grown in soils from Albany or Fox Park, Wyoming. Treatments which do not share a common letter are significantly different ($p < 0.05$). A significant quadratic decrease in pre-dawn water potential ($p < 0.05$) occurred in Albany seedlings exposed to simulated nitric acid rain. There was no significant effect of simulated nitric acid rain on the pre-dawn water potentials of Fox Park seedlings ($p = 0.06$).


Albany Seedlings
Height (mm)
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
a b
a b
a
b
c
c
30x HCL
50x HCL
AMBIENT
10x NO3
30x NO3
50x NO3
Treatment

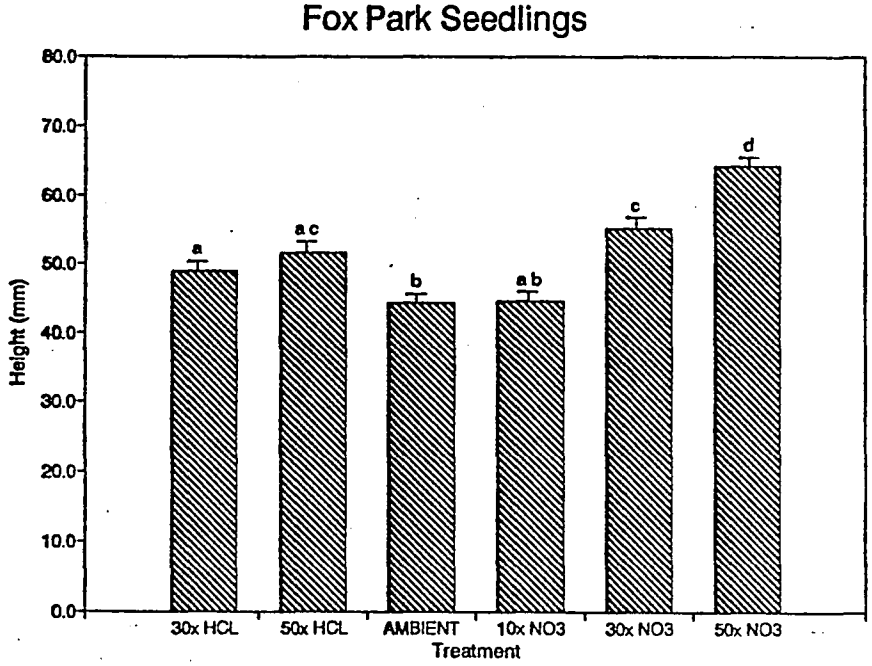
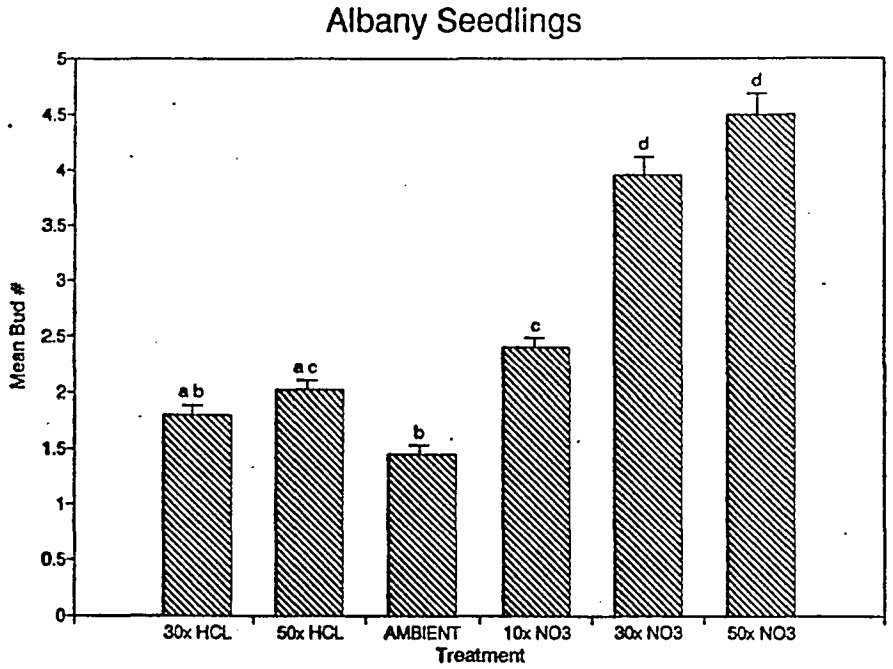

Fox Park Seedlings
Height (mm)
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
a
a c
b
a b
c
d
30x HCL
50x HCL
AMBIENT
10x NO3
30x NO3
50x NO3
Treatment

Figure 1


Albany Seedlings
Mean Bud #
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
a b
a c
b
c
d
d
30x HCL
50x HCL
AMBIENT
10x NO3
30x NO3
50x NO3
Treatment

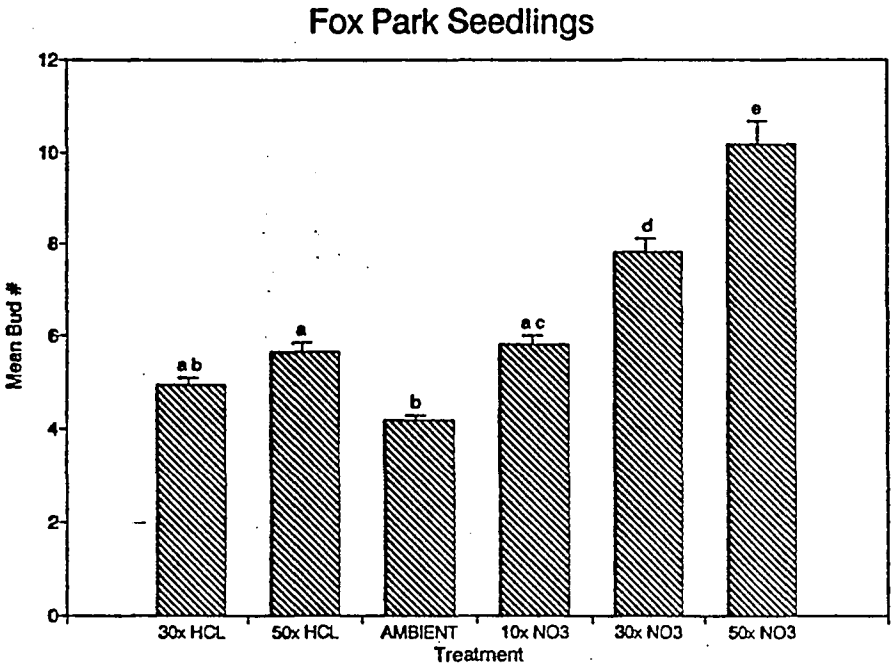
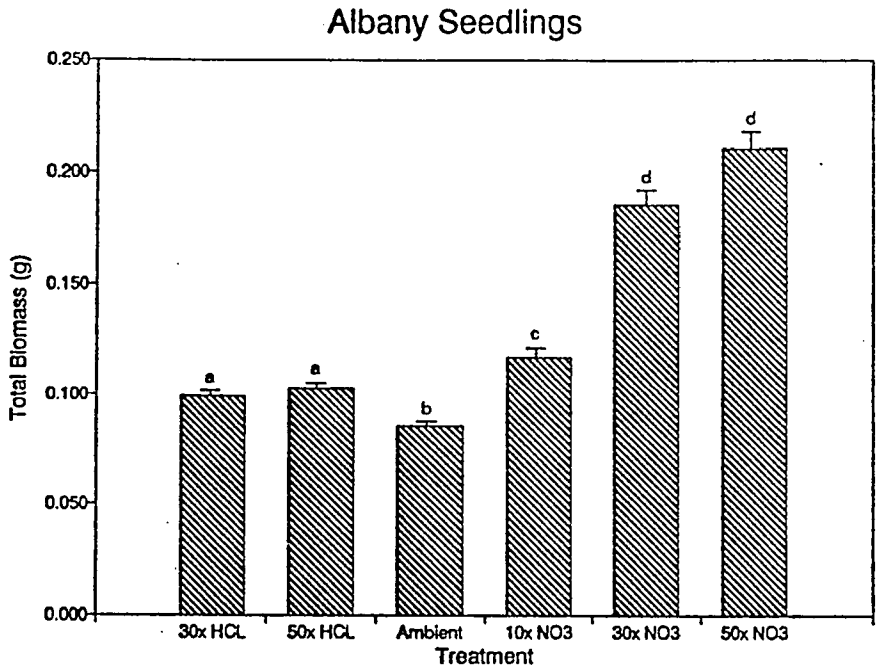

Fox Park Seedlings
Mean Bud #
0
2
4
6
8
10
12
a b
a
b
a c
d
e
30x HCL
50x HCL
AMBIENT
10x NO3
30x NO3
50x NO3
Treatment

Figure 2


Albany Seedlings
Total Biomass (g)
0.250
0.200
0.150
0.100
0.050
0.000
a
a
b
c
d
d
30x HCL
50x HCL
Ambient
10x NO3
30x NO3
50x NO3
Treatment

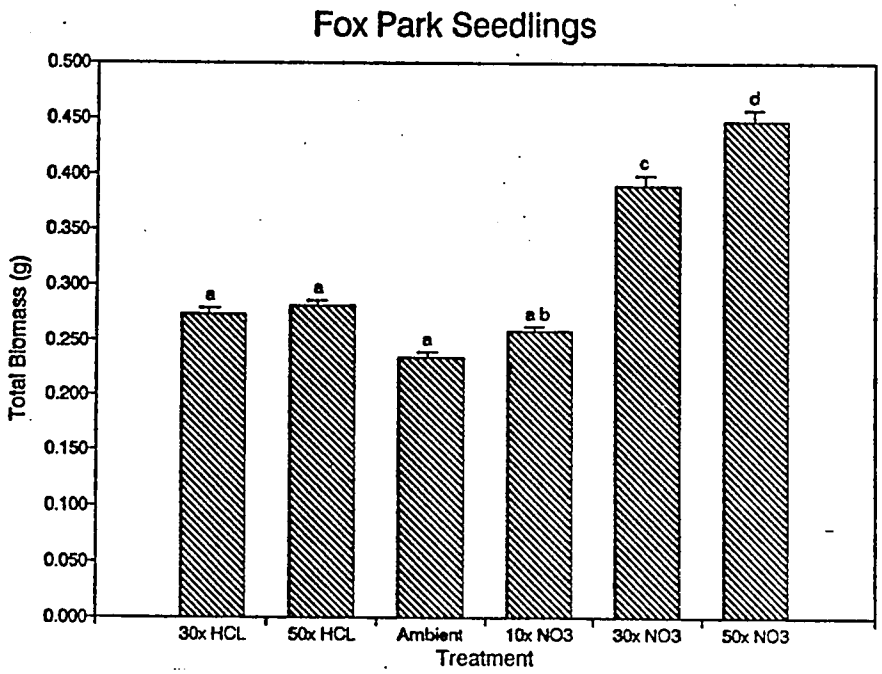
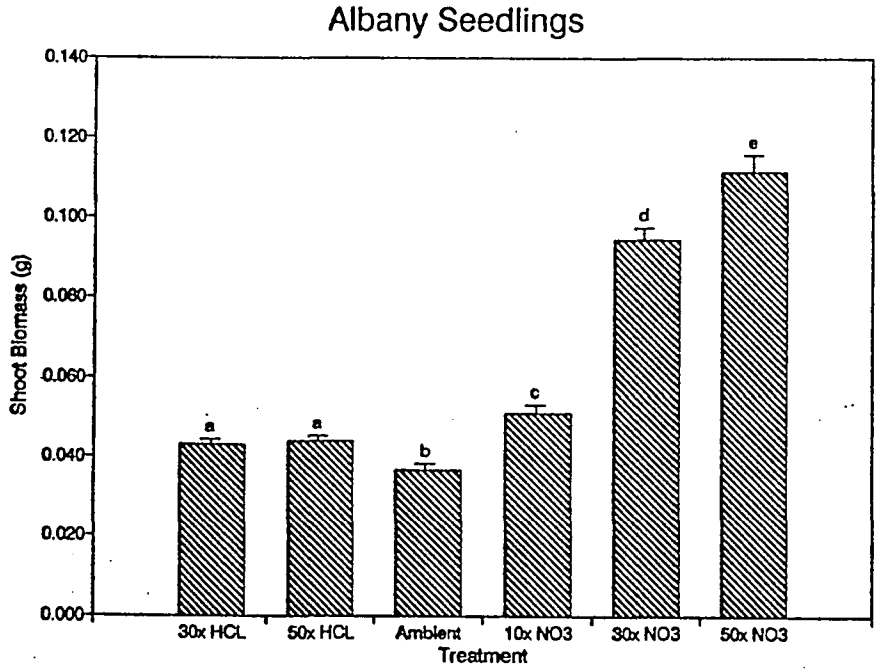

Fox Park Seedlings
Total Biomass (g)
0.500
0.450
0.400
0.350
0.300
0.250
0.200
0.150
0.100
0.050
0.000
a
a
a
a b
c
d
30x HCL
50x HCL
Ambient
10x NO3
30x NO3
50x NO3
Treatment

Figure 3


Albany Seedlings
Shoot Biomass (g)
0.140
0.120
0.100
0.080
0.060
0.040
0.020
0.000
a
a
b
c
d
e
30x HCL
50x HCL
Ambient
10x NO3
30x NO3
50x NO3
Treatment

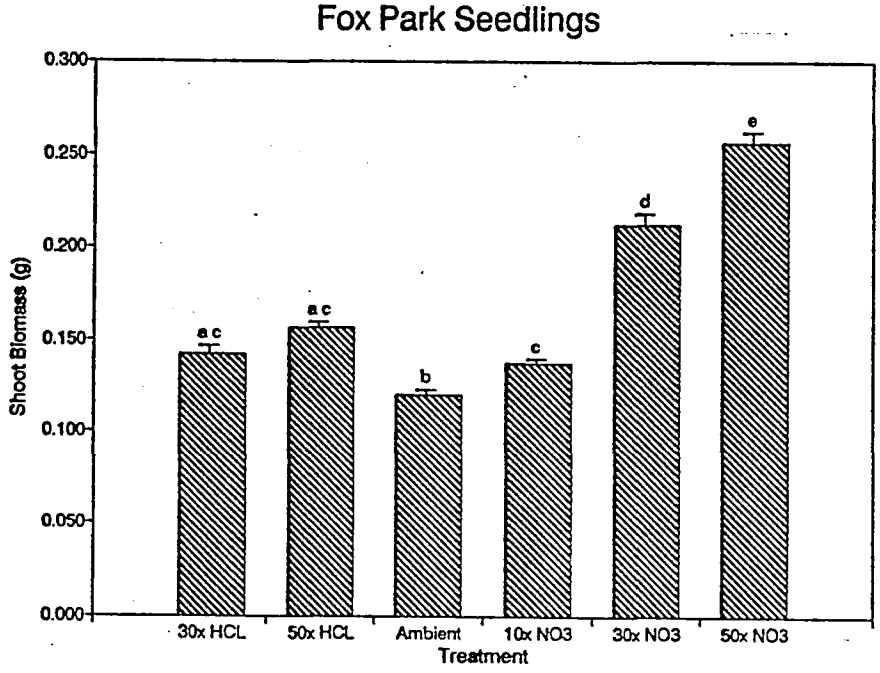
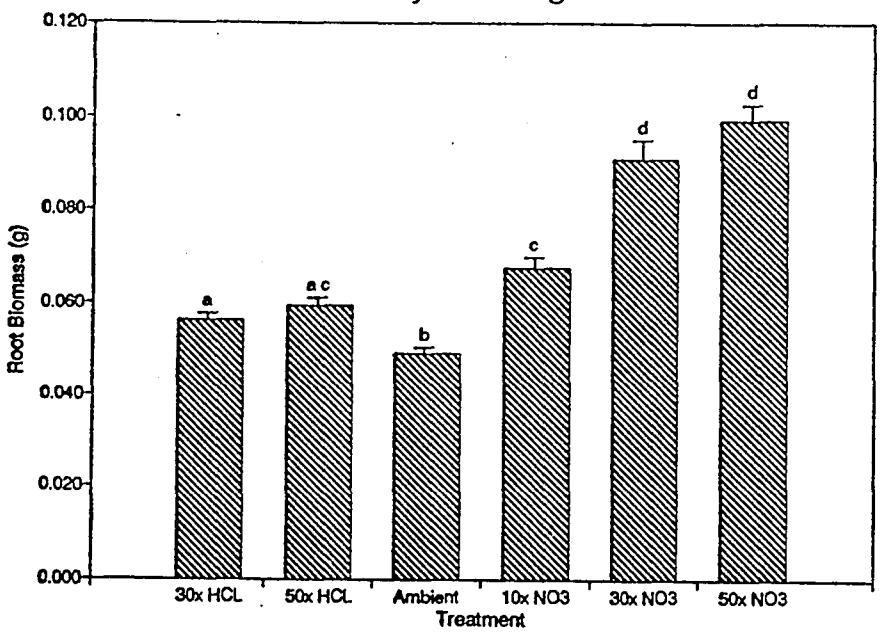

Fox Park Seedlings
Shoot Biomass (g)
0.300
0.250
0.200
0.150
0.100
0.050
0.000
a c
a c
b
c
d
e
30x HCL
50x HCL
Ambient
10x NO3
30x NO3
50x NO3
Treatment

Figure 4


Albany Seedlings
Root Biomass (g)
0.120
0.100
0.080
0.060
0.040
0.020
0.000
a
a c
b
c
d
d
30x HCL
50x HCL
Ambient
10x NO3
30x NO3
50x NO3
Treatment

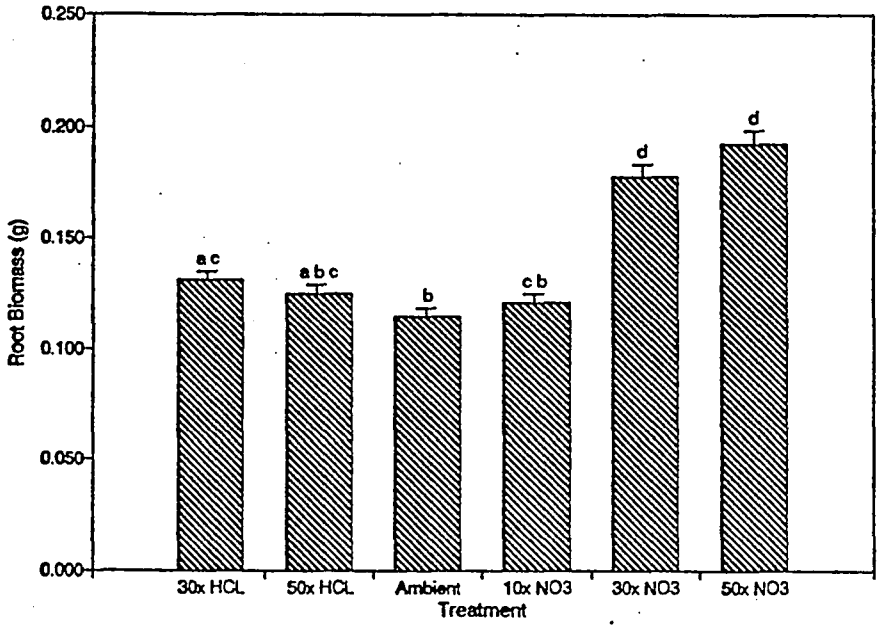
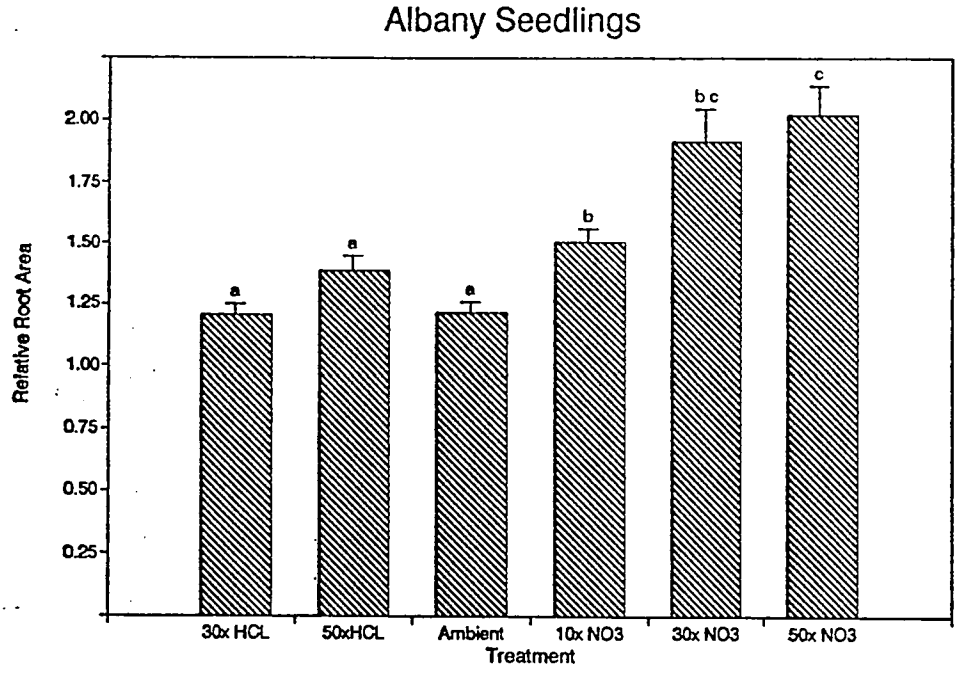

Fox Park Seedlings
Root Biomass (g)
0.250
0.200
0.150
0.100
0.050
0.000
a c
a b c
b
c b
d
d
30x HCL
50x HCL
Ambient
10x NO3
30x NO3
50x NO3
Treatment

Figure 5


Albany Seedlings
Relative Root Area
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
a
a
a
b
bc
c
30x HCL
50xHCL
Ambient
10x NO3
30x NO3
50x NO3
Treatment

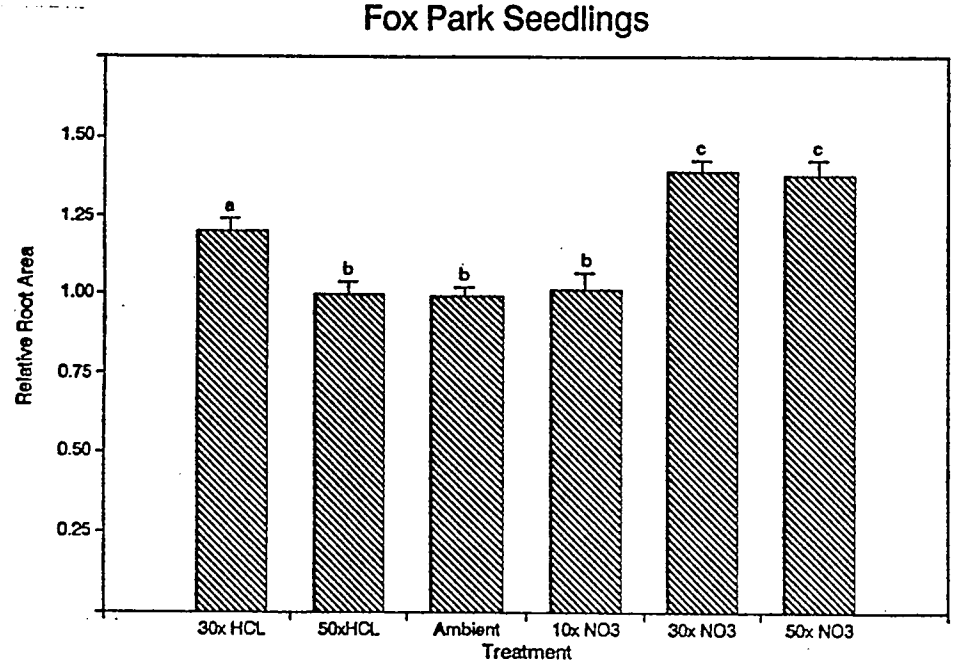
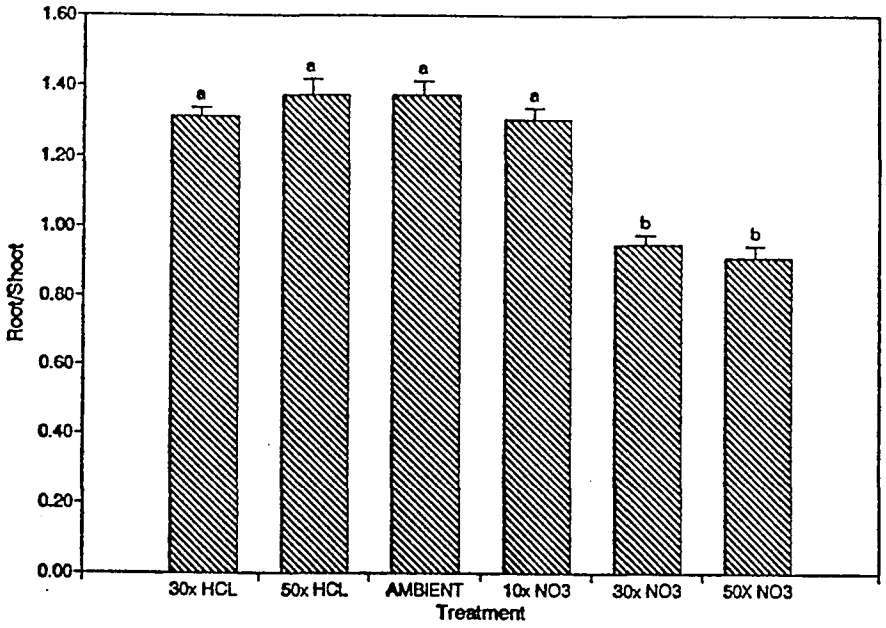

Fox Park Seedlings
Relative Root Area
1.50
1.25
1.00
0.75
0.50
0.25
a
b
b
b
c
c
30x HCL
50xHCL
Ambient
10x NO3
30x NO3
50x NO3
Treatment

Figure 6


Albany Seedlings
Root/Shoot
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
a
a
a
a
b
b
30x HCL
50x HCL
AMBIENT
10x NO3
30x NO3
50X NO3
Treatment

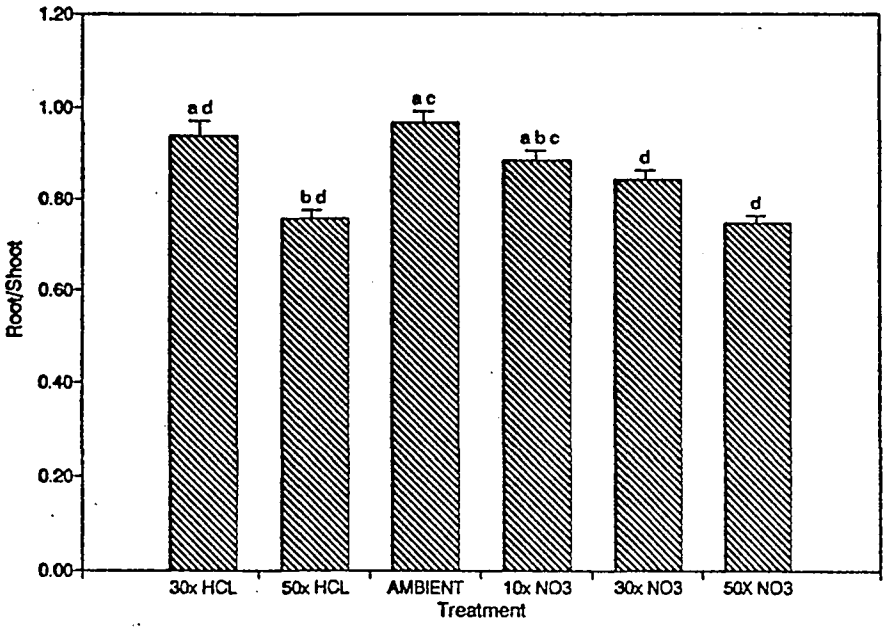
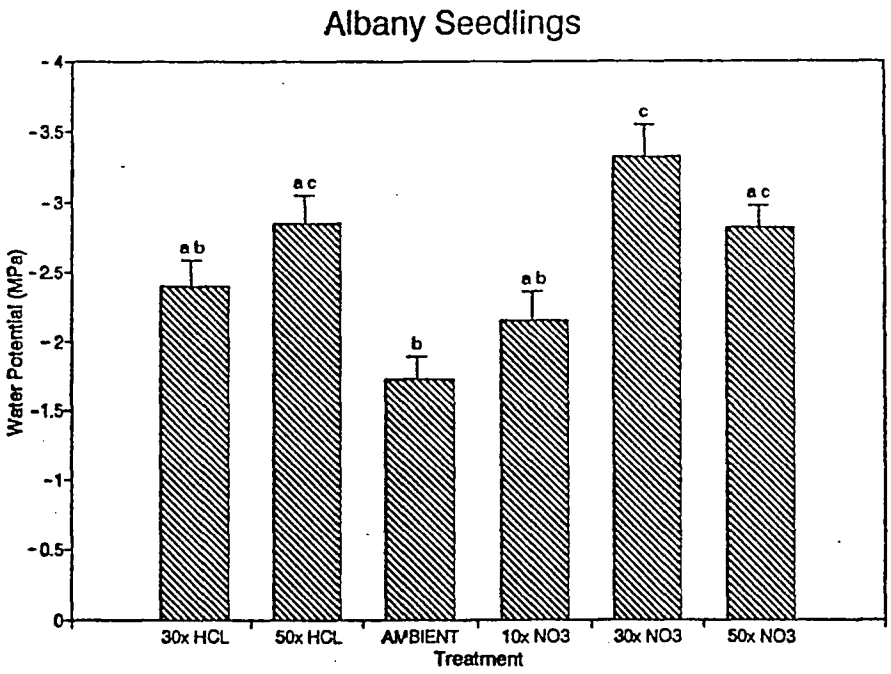

Fox Park Seedlings
Root/Shoot
1.20
1.00
0.80
0.60
0.40
0.20
0.00
a d
b d
a c
a b c
d
d
30x HCL
50x HCL
AMBIENT
10x NO3
30x NO3
50X NO3
Treatment

Figure 7


Albany Seedlings
Water Potential (MPa)
-4
-3.5
-3
-2.5
-2
-1.5
-1
-0.5
0
a b
a c
b
a b
c
a c
30x HCL
50x HCL
AMBIENT
10x NO3
30x NO3
50x NO3
Treatment

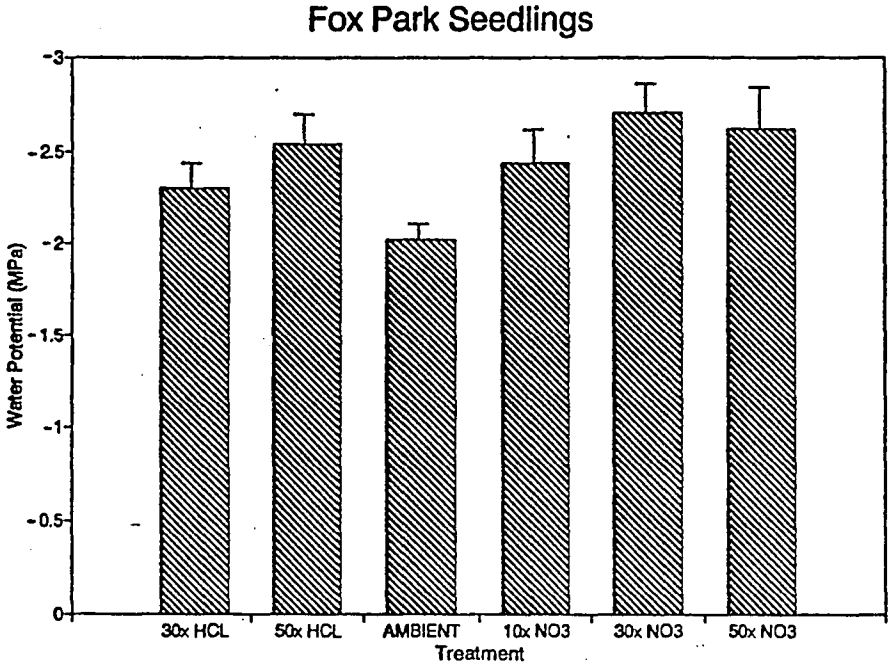

Fox Park Seedlings
Water Potential (MPa)
-3
-2.5
-2
-1.5
-1
-0.5
0
30x HCL
50x HCL
AMBIENT
10x NO3
30x NO3
50x NO3
Treatment

Figure 8